DOLPHIN HABITATS IN THE EASTERN TROPICAL PACIFIC

David W. K. Au and Wayne L. Perryman[1]

ABSTRACT

Research-ship surveys by the Southwest Fisheries Center provided information on the distributions of spotted, spinner, striped, and common dolphins in the eastern tropical Pacific. The main surveys were conducted from January to March during 1976, 1977, 1979, and 1980. Two ships were used per survey, and together they overlapped most areas in the eastern Pacific where dolphins and yellowfin tuna are jointly fished by purse seiners.

The spatial distribution of sightings and of sighting rate of these species show a complementarity to their patterns, although there is a broad overlap. Spotted and spinner dolphins occurred primarily in tropical waters north of the Equator, but also in the seasonal tropical waters south of the Galapagos Islands. These dolphins were relatively infrequent along the Equator, off Costa Rica, and northern South America. Common and striped dolphins tended to be more frequent in these same areas of less frequent spotted and spinner dolphins.

The differences in habitats of these two species pairs can be described in oceanographic terms. Spotted and spinner dolphins are primarily in Tropical Surface Water, centered off southern Mexico and extending westward along lat. 10°N, where thermocline "ridging" and relatively small annual variations in surface temperature are features. Common and striped dolphins appear to perfer equatorial and subtropical waters with relatively large seasonal changes in surface temperature and thermocline depth and with seasonal upwelling.

The species composition of various areas in the eastern tropical Pacific supports the contention of two major communities. South of where spotted and spinner dolphin schools predominate (along with Risso's, bottlenose, and rough-toothed dolphins), striped and common dolphins and also pilot whales become increasingly important. Observations along the Equator also suggest a fauna different from that of the Tropical Surface Water that is most characterized by spotted and spinner dolphins.

A trophic basis to these faunal differences is suggested by the interactions with fish and birds. Assuming the birds indicate co-occurring tuna, only the spotted and spinner dolphins are commonly found with fish. The distribution of these dolphins as they co-occur with bird flocks and tuna indicates that this interspecific association is confined primarily to the Tropical Surface Water and is a characteristic feature of its epipelagic community.

The eastern tropical Pacific Ocean supports productive tuna fisheries as well as an abundant and diverse cetacean fauna. Tuna fishermen there take advantage of the fact that tuna and dolphins frequently swim together. In the "porpoise-tuna" fishery for yellowfin tuna, *Thunnus albacares*, spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, are temporarily caught by purse seiners in order to take the associated tuna. Striped and common dolphins, *S. coeruleoalba* and *Delphinus delphis*, are caught to a lesser extent for the same reason. These dolphins suffer incidental mortality in the fishery and, because of the resulting concern, the Southwest Fisheries Center has been studying their populations to better advise on their management (Smith 1983). Learning about their habitats is one aspect of these studies.

Perrin (1975a), using the information collected mainly aboard tuna seiners, first showed that the geographic distributions of spotted, spinner, and striped dolphins in the eastern Pacific are extensive, stretching westward from the American coasts past long. 145°W at about lat. 10°N and also dipping south and southwest of the Galapagos Islands. Evans (1975) showed that the common dolphin occurs offshore of Central America to about long. 112°W and also along the Equator, westward past the Galapagos Islands. Recent summaries of available information (Au et al. 1979[2]; Scott 1981; Perrin et al. 1983) have shown that the distributions of these dolphins are even more extensive than originally perceived. Indeed the species have been reported from localities across the entire Pacific (Alverson 1981).

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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The purpose of this paper is to describe the January-March distributions of schools of spotted, spinner, striped, and common dolphins as determined from research ship surveys. Being independent and distinct from data collected by observers aboard tuna seiners, these survey data enable a separate evaluation of habitats and ecological relationships. The distributions derived will be discussed in terms of habitat features and interspecific associations including those of other cetaceans, yellowfin tuna, and certain seabirds. We propose that two major cetacean communities can be recognized, centered broadly about the tropical and about the equatorial-subtropical surface water provinces (Fig. 1).

METHODS

The Southwest Fisheries Center conducted or participated in 17 research cruises studying cetaceans between 1976 and 1981. Eight major cruises were carried out between January and March of 1976, 1977, 1979, and 1980, with the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. During these surveys, schools of all cetacean species encountered (at least 23 species in the areas of interest) were approached to allow close observation. The combined cruise tracks of these January-March surveys formed an extensive coverage of the eastern tropical Pacific and included areas not frequently searched by fishing vessels (Fig. 2). The latter are the equatorial waters and areas both south of lat. 8°N and west of long. 110°W. The cruise tracks during any particular year were chosen to investigate certain aspects of dolphin distribution, e.g., the intensive surveys during 1979 off southern Mexico and central America constituted a joint aircraft-ship survey of the nearshore habitat. The remaining other nine cruises were either for special studies or of ships of opportunity. In the latter case, the ships did not usually divert course to inspect cetacean schools that were sighted.

Cetacean observations from a research ship were conducted by scanning the waters ahead and to the sides of the ship through 20 × 120 mm USN MK-3

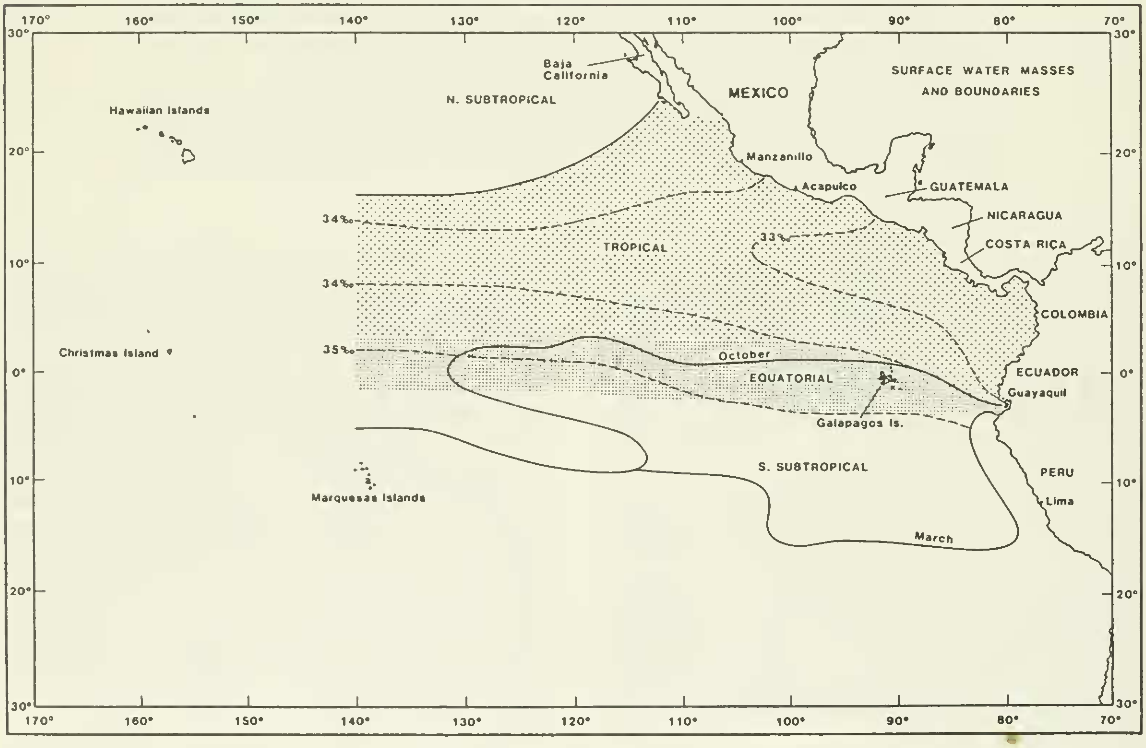

FIGURE 1.—Surface water masses and boundaries of the tropical ocean in the eastern Pacific, based on Wyrtki's (1964a, 1967) analysis to long. 140°W. Boundaries are a function of the 24°C surface isotherm and the 1°C/10 m thermocline gradient. Notice that in October the southern boundary to the eastern tropical ocean lies mostly north of the Equator, while in March this boundary lies far to the south so that southern subtropical waters become tropical.

or 25 × 150 mm Fuji binoculars, mounted both port and starboard either on or above the flying bridge. The sighting distance to the horizon was about 7.0 and 5.5 nmi for the *David Starr Jordan* and *Townsend Cromwell* respectively. Both ships cruised at about 10 kn (18.5 km/h). The cetacean search-day generally started at 0600 and ended 1800, with two teams, or watches, alternating. In 1976 and 1977 the watches were each 2 or 3 h long, depending on the ship. In 1979 and 1980 they were all standardized to 3 h. There were two experienced persons on each watch, who alternated each hour between the port and starboard binoculars. A third person sometimes helped in record keeping, obtaining supplementary data, and temporarily relieving the other watch members. The peripheral data collected included bathythermograms, surface temperature and salinity, weather observations, sighting condition measurements, sighting effort, and observations on fish and birds.

When a cetacean school was sighted, its angle relative to the ship's heading was measured and its distance from the ship estimated. The ship then approached the school for closer observation. School size was estimated and the species identified.

The reader is cautioned that the distributions to be described are based upon relatively few sightings of schools (Table 1) and that they pertain to the January-March season specifically. Though the pattern of sampling was widespread, the actual area surveyed was a very small fraction of the huge area

TABLE 1.—Summary of school sizes for spotted, spinner, striped, and common dolphins from the January-March research cruises of 1976, 1977, 1979, and 1980.

	Arithmetic			Geometric	
Species	n	$\bar{x}$	s	$\bar{x}$	s[1]
Spotted[2]	157	148.52	300.93	65.55	3.56
Spotted and spinner	79	357.42	444.50	211.67	2.93
Spinner[3]	44	228.39	291.54	107.05	3.88
Striped	187	60.84	69.78	40.74	2.56
Common	98	261.16	484.64	108.47	3.72
Total[4]	565				

[1]Standard deviation factor for the geometric mean.
[2]Total spotted dolphin schools is 157 + 79 = 236.
[3]Total spinner dolphin schools is 44 + 79 = 123.
[4]Additionally, there were 838 school sightings of unidentified and other species of dolphins (Delphinidae) and 543 school sightings of whales (Balaenopteridae, Ziphiidae, and Physeteridae).

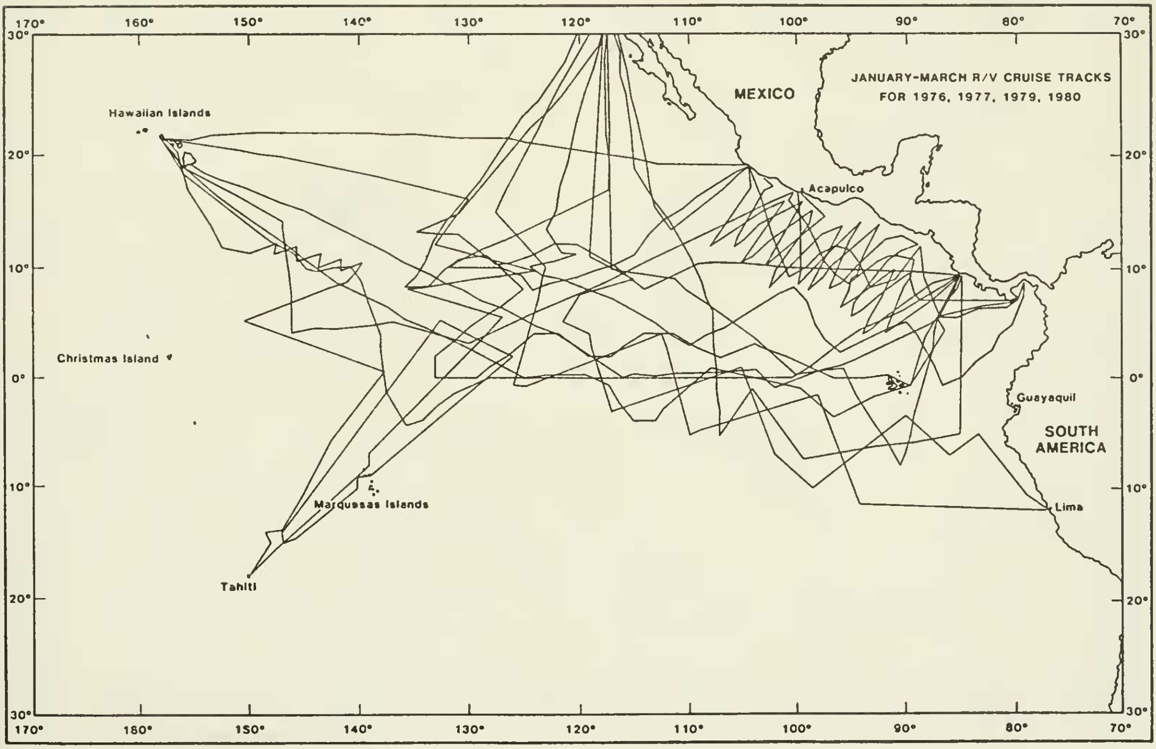

FIGURE 2.—Cruise tracks of the January-March cruises by RV *David Starr Jordan* and RV *Townsend Cromwell*. These cruises took place in 1976, 1977, 1979, and 1980.

of the eastern Pacific. The patterns of species distribution we describe will not always be obvious. Nevertheless there is evidence from other distribution studies, using data collected from the fishery, that these patterns are real (Perrin et al. 1983).

The results described in this paper are based upon our personal experiences at sea where the procedure of investigating all cetacean schools and continuously monitoring the physical and biotic environment enabled the development of an ecological understanding of these dolphins. Continuity in these studies was provided by the fact that on each ship there was at least one experienced observer who participated during all cruise years. We present our results as an independent, research-ship based, assessment of species distributions and habitat areas.

RESULTS

Distribution and Relative Abundance of Dolphin Schools

Plots of the sighting localities of schools of spotted, spinner, striped, and common dolphins, obtained during the January-March research cruises, show the geographical distributions of these species during the northern winter season. Table 1 summarizes the numbers and sizes of the schools which were identified and studied. Geographic locations referred to in the text can be found in Figure 1.

Spotted and spinner dolphins are often in mixed schools (33.5% of spotted dolphins schools also contained spinner dolphins, Table 1), and so the sightings of spotted or of mixed spotted plus spinner dolphin schools are shown together (Fig. 3). Most of the mixed schools were encountered off southern Mexico, where the eastern form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) usually accompanied spotted dolphins (cf. Figs. 3, 4). Mixed schools were uncommon along the Equator, as was the spotted dolphin itself, especially west of long. 110°W. Large schools (>300 individuals) of spotted dolphin were widely scattered, but tended to be more common off southern Mexico. Westward extensions of distribution appeared to occur as three main lobes: about lat. 10°n, between lat. 0° and 5°N, and between lat. 2°S and 5°S.

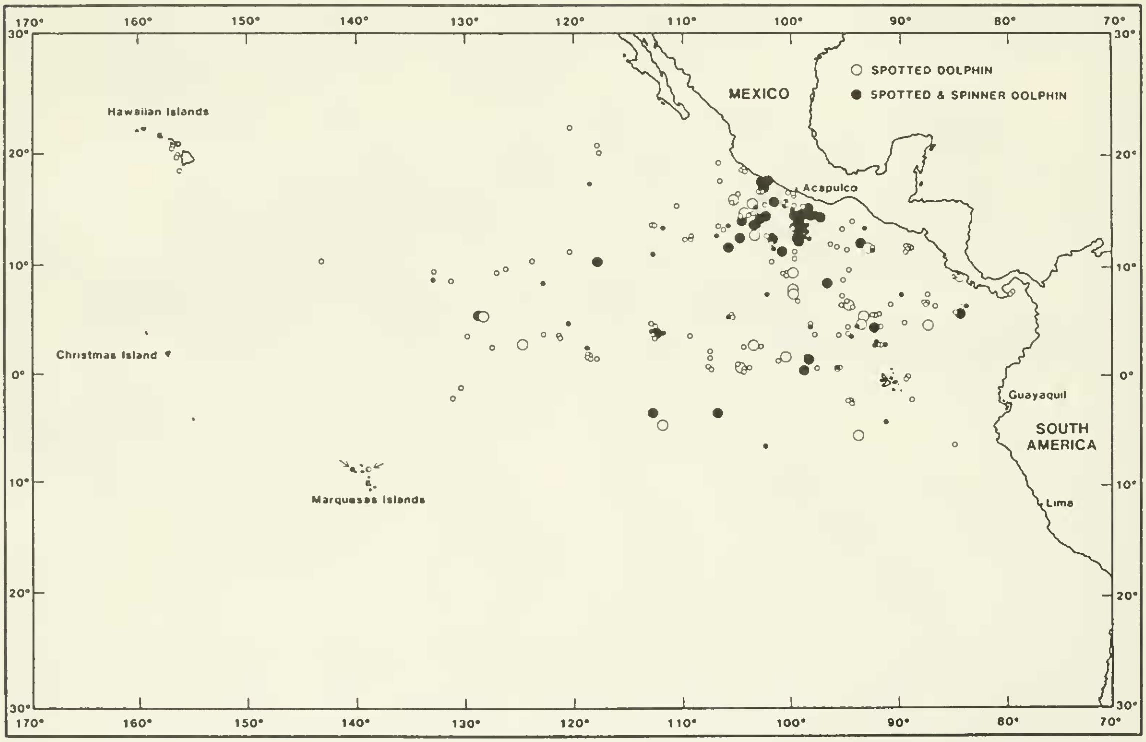

FIGURE 3.—Distribution of spotted and spotted plus spinner dolphin schools seen during the January-March research cruises. Larger circles indicate schools of >300 animals.

The spinner dolphin appears to be distributed like the spotted dolphin, with westerly extending lobes of distribution in similar latitudes (Fig. 4). Schools were infrequent along the Equator, more so than were those of spotted dolphin. The eastern spinner was encountered frequently off southern Mexico, where its main population center appeared to be relatively localized. However, eastern spinner dolphins were seen as far offshore as long. 126°W near lat. 10°N and also nearly to the Equator within a broad, 600 nmi coastal belt off Central America. The whitebelly form of spinner dolphin (Perrin 1975a, b; Perrin et al. 1977) occurred in a broad range north and south of the Equator and at the southern and western portions of the total spinner dolphin range. Large schools (>300) were seen mostly off southern Mexico (eastern spinner) and south of the Equator (whitebelly spinner).

Striped and common dolphins seem to have a distribution pattern qualitatively different from that of spotted and spinner dolphins (Fig. 5). A distinct distributional lobe, consisting primarily of common dolphins, occurred off Baja California, with extensions around the Revilla Gigedo Islands (ca. lat. 19°N, long. 111°W). Between lat. 5° and 12°N, off Central America, there was a second lobe made up of both species. This lobe attenuated to the west along lat. 10°N, but appeared to re-intensify past long. 130°W. Only striped dolphins were seen in the intermediate interval between long. 100°W and 130°W along this lobe. A third lobe appeared to originate off Peru. It merged somewhat with the outer portions of the Central American lobe, and then extended westward along the Equator. Equatorial waters were frequented by both species out to about long. 100°W, beyond which striped dolphins apparently predominate. The striped dolphin is the more widespread of the two species; however, its school sizes are small (Table 1). Large schools (>300) of the common dolphin occurred within each of the three main centers of its distribution.

The above sighting data were adjusted to show the distributions of relative abundance of schools by correcting for searching effort. Effort is calculated as miles searched = time searched × ship speed. Relative abundance of schools was expressed as schools per 100 nmi searched (approximately the

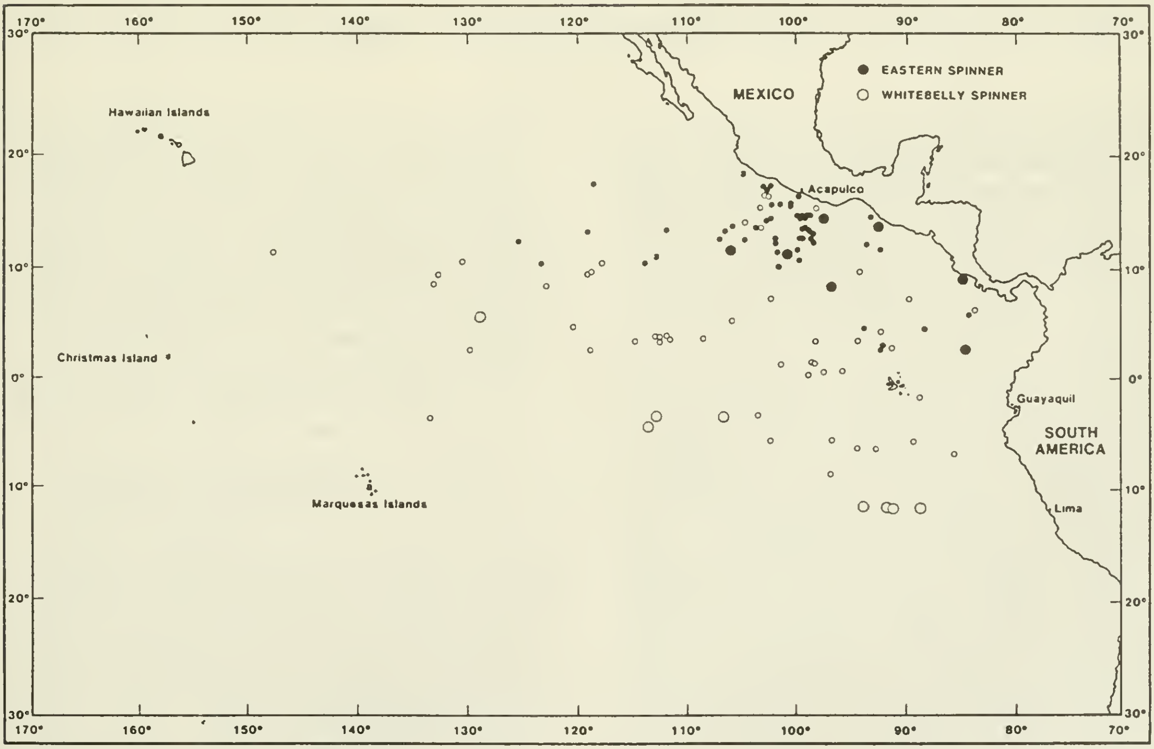

FIGURE 4.—Distribution of spinner dolphin schools, eastern and whitebelly forms, seen during the January-March research cruises. Larger circles indicate schools >300 animals.

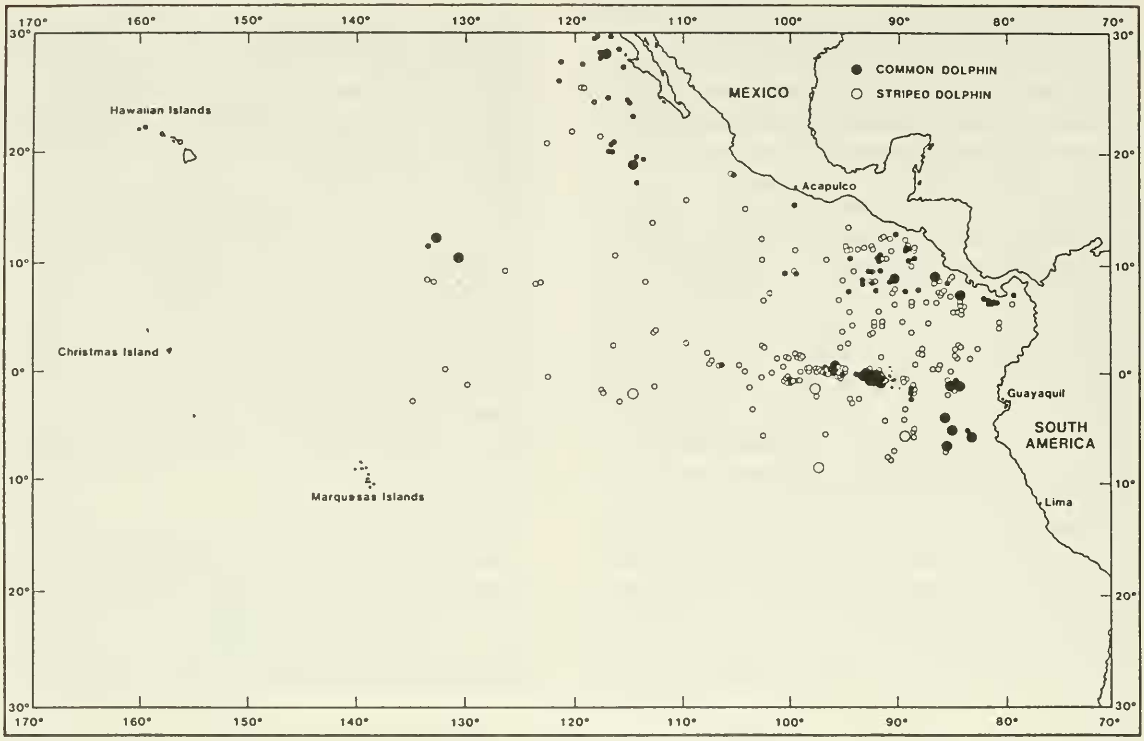

FIGURE 5.—Distribution of striped and common dolphin schools seen during the January-March research cruises. Larger circles indicate schools >300 animals.

distance searched during 1 d). Data for days during which the Beaufort wind force was equal to 4 (11-16 kn) for more than 50% of the time, or averaged more than 4, were not used. Only schools sighted at distances not more than 3 perpendicular nmi from the ship's track and not more than 5 radial nmi distant were considered, to reduce the effects due to distance on sightability. The latter criterion was not applied to the 1976 cruises, because the radial distances then were frequently overestimated. An areal smoothing procedure that consisted of calculating the average number of schools per 100 mi searched within sequential, overlapping 5° squares was employed. Sequential squares were offset 2.5° in latitude and longitude, so that each was wholly overlapped by 25% of the area of each of four adjacent squares. A day's sighting rate was assigned to a particular square if more than 50% of the search effort occurred therein, and the value was plotted at the center point of that square. If the search effort fell equally in two squares, the day's results were assigned to both squares. These moving, areal means of sightings per 100 nmi searched were plotted and contoured. Contouring (and interpolation) constituted a second level of areal smoothing.

The maps so generated describe the distribution of relative abundance of species schools as surveyed during January to March. These relative abundance data were combined for spotted and spinner dolphins and for striped and common dolphins, both because these species pairs had similar distributions and because pooling gave desirable sample sizes.

The combined spotted and spinner dolphin map (Fig. 6) shows some patterns already noted from the school distribution. These schools appeared relatively more abundant off southern Mexico (mostly spotted and eastern spinner dolphins) and again along an east-west band just north of the Equator, especially west of long. 105°W. Another band of greater abundance occurred south of the Equator. Spotted and spinner dolphins appeared less abundant just west of Costa Rica, off the coast of northern South America, and along the Equator. A weak lobe of higher relative abundance extended west of long. 120°W broadly about lat. 10°N.

Striped and common dolphins show a relative abundance pattern in which areas of higher density tend to be complementary to that of spotted and

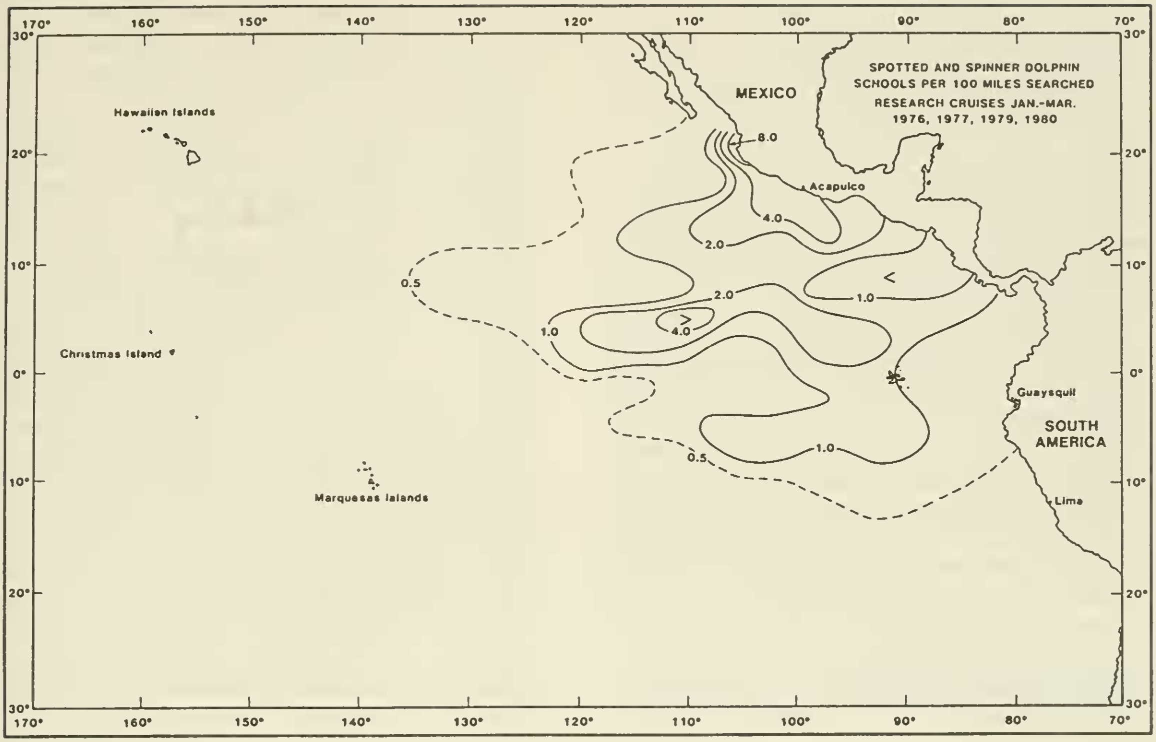

FIGURE 6.—Distribution of relative abundance of spotted and spinner dolphins, inferred from data of the January-March research cruises. Hawaiian and Marquesan sightings are not considered.

spinner dolphins (Fig. 7). Conspicuous lobes extended from off Baja California and also broadly from the coasts of Central America and northern South America out to and along the Equator. Within the latter lobe, centers of higher relative abundance occurred west of Nicaragua and Costa Rica and west of the Galapagos Islands, all areas where reduced abundance of spotted and spinner dolphins occurred. The Galapagos area and the lobe off Baja California were dominated by the common dolphin (cf. Fig. 5).

Dolphins of Tropical Water and Upwelling-Modified Water Habitats

The areas of greater frequency of spotted and spinner dolphins during January-March are the typical tropical waters of the eastern tropical Pacific. These waters are underlain by a sharp thermocline, generally >2°C/10 m, at depths usually much <50 m. The surface temperatures are >25°C, and the salinities <34‰. Such tropical waters are defined by Wyrtki (1966, 1967) as Tropical Surface Water (see Fig. 1). In particular the warm "Inner Tropical" Waters (Wyrtki 1964a) lying primarily north of the Equator comprise the major habitat of spotted and spinner dolphins (Fig. 6). The waters south of the Equator, where the relative abundance of these dolphins is also higher, are seasonally tropical, and are therefore called southern Subtropical Surface Water (Wyrtki 1966, 1967). These waters, occurring approximately south of lat. 2.5°S, have surface salinities >35‰, and during January-March (southern summer), warm to more than 26°C over a shallow, sharp thermocline. Since spotted and spinner dolphins occur there frequently, at least during January-March, it appears that spotted and spinner dolphins prefer all waters whose characteristics are, or become, tropical in the eastern Pacific. However the primary habitat appears to be the "Inner" Tropical Waters north of the Equator.

In contrast striped and common dolphins appear to prefer waters with more variable conditions during January-March. Their most important habitat appears to be broadly centered about equatorial waters (Fig. 7). This band of distribution extends into the central Pacific along the Equator. In the east it broadens widely to include Tropical Water off Central America and Subtropical Water off Peru. The equatorial distribution is in Equatorial Surface Water (Wyrtki 1966, 1967), a transitional water mass straddling the Equator and characterized by salinities between 34 and 35‰, upwelling, and a relatively weak thermocline. These waters are markedly cooled from June to December (southern winter-spring) by increased upwelling and by advection from the Peru Current. In the Subtropical Water habitats of striped and common dolphins, both off Peru and Baja California, there are also large seasonal changes in temperature structure and effects from upwelling. Finally the Tropical Water habitat in the Central American Bight is notably variable (below).

The waters we call the "Central American Bight" (roughly, the near coastal waters from Guatemala to Ecuador) constitute the most important area of overlap for spotted, spinner, striped, and common dolphins, but this overlap is not balanced among the species. These waters are tropical, but they are the most variable within the Tropical Surface Water province. The Equatorial Countercurrent, flowing eastward between lat. 4°N and 10°N, terminates and turns there, creating a complex circulation. The annual north-south migration in these latitudes of the Intertropical Convergence Zone, where north and south trade winds meet, bring southerly winds, rain, reduced salinity, and an intensified Countercurrent during the second half of the year (Bennett 1966; Wyrtki 1967, 1974; Forsebergh 1969). Later during the northern winter (January-March), northeasterly winds blow across Central America from the Atlantic, producing coastal upwelling, wind stirring, and more complex temperature patterns. The Costa Rica Dome, a localized, offshore upwelling at about lat. 8°N, long. 90°W (Wyrtki 1964b), also may be seasonally intensified (Hofmann et al. 1981).

These variable Central American Bight waters appear to have more abundant schools of striped and common dolphins than of spotted and spinner dolphins (cf. Figs. 3-7). It seems that all areas with greater concentration of striped and common dolphins have highly variable oceanographic features that are "upwelling-modified".

In spite of the rather strong overlap in distribution among the four dolphin species in the Central America Bight, the biogeographic distinction, including the relationships to environment, between

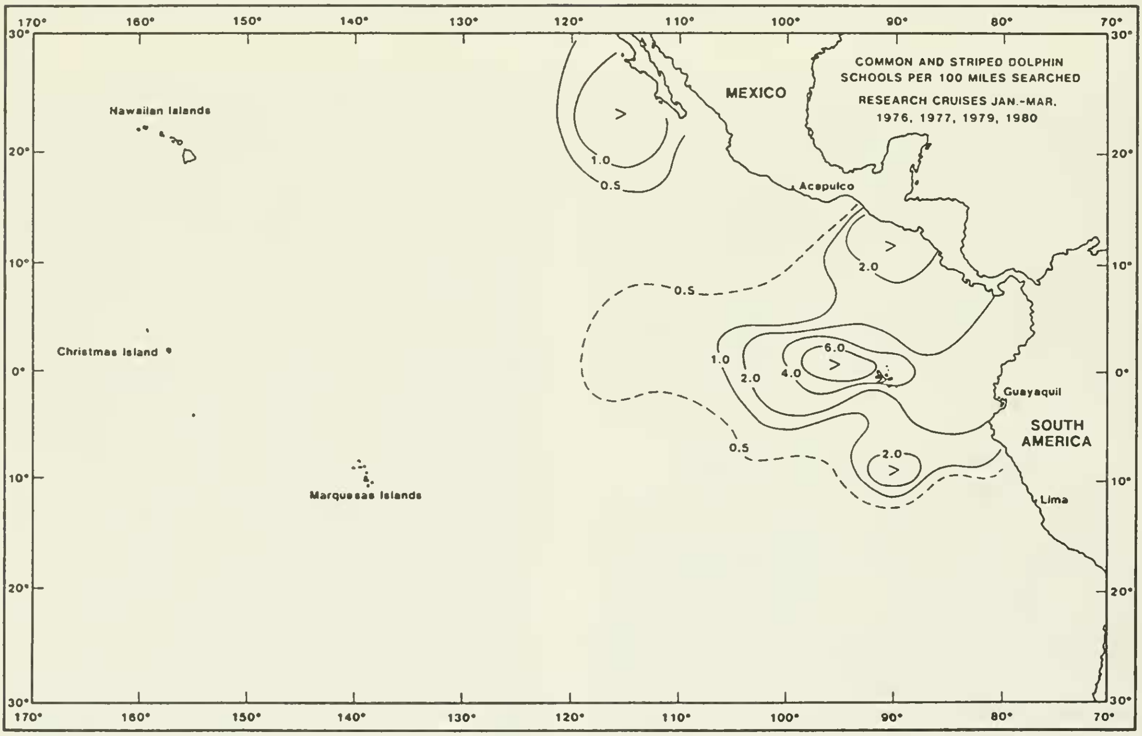

FIGURE 7.—Distribution of relative abundance of striped and common dolphins, inferred from data of the January-March research cruises.

the spotted and spinner dolphins of the Tropical Water and the striped and common dolphins of the Upwelling-Modified Water may be quite apparent. This was the case during the intensive winter surveys of 1979 in the Central American Bight, shown in Figure 8. Superimposed in the figure are contours of the 20°C isotherm depth (essentially the thermocline depth) which were obtained from expendable bathythermograph probes dropped at 30-60 mi intervals (55.6-111.1 km). Notice that spotted and spinner dolphins were encountered mainly off southern Mexico, where the deeper 20°C isotherms indicated the occurrence of a large surface lens of warm water. The warmest surface waters in the eastern tropical Pacific normally occur in this area; the thermocline gradient is weaker, and the annual variation in surface temperature is relatively small (Wyrtki 1964a). In the more variable tropical waters of the Central American Bight, where the thermocline had shoaled or ridged to <60 m, both these species were seen too. However, striped and common dolphin schools predominated, especially near the shallower isotherms that mark the location of the Costa Rica Dome. Finally the equatorial distribution of primarily striped and common dolphins was evident. The sampling suggested that Subtropical Waters south of the Galapagos Islands were probably also important to these latter two species. A 1977 aerial survey of cetaceans in these waters off Central America (SWFC 1977[3]) obtained results similar to those just described.

Though there appear to be large-scale geographic differences in the habitats of spotted and spinner dolphins and of striped and common dolphins, there was no evidence of negative association among these species. The frequency of days in the Central American Bight, both in 1979 and 1980, with different combinations of these species encountered, are summarized in Table 2. There was no evidence, using chi-square contingency tests for association among spotted and/or spinner dolphins and striped or common dolphins, that the species were not occurring independently on any particular day.

Our contention that spotted and spinner dolphins and striped and common dolphins differentially inhabit waters of different oceanographic characteris-

[3]Southwest Fisheries Center (SWFC). 1977. Aerial survey trip report January - June 1977. Admin. Rep. No. LJ-78-01, 73 p. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

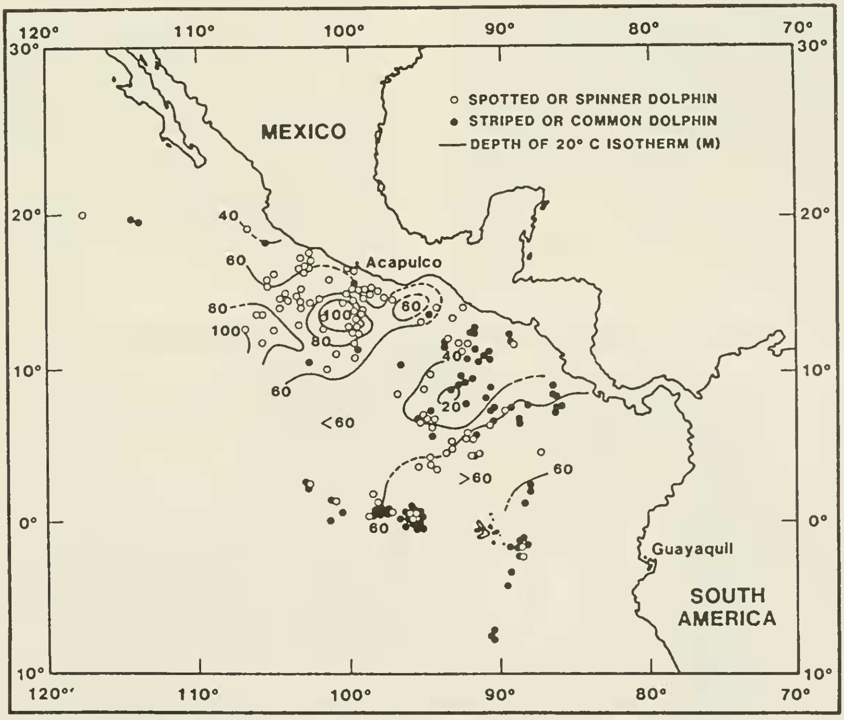

FIGURE 8.—Distribution of dolphin schools by species type in the Central American Bight, with reference to the depth of the 20°C isotherm. Data are from the January-March cruises of 1979.

TABLE 2.—Number of days according to combinations of four species of dolphins that were encountered in the Central American Bight.

		Spotted and/or spinner				Striped		Common	
Year	Area[1]	Alone	With striped	With common	With striped + common	Alone	With common	Alone	None of these spp.
1979	N	17	2	0	0	1	1	1	6
	S	6	7	0	4	6	1	6	8
1980	N	9	2	0	0	0	0	0	0
	S	5	5	1	4	6	3	3	7

[1]Northern (N) and southern (S) areas are partitioned to illustrate species differences by area; the dividing line is perpendicular to the coast at lat. 16°N.

tics is supported by physical environmental measurements. The data indicated a species differential with respect to waters with temperature ⩾25°C and salinities ⩽34.5‰, and waters of <25°C and >34.5‰. The former is primarily Tropical Surface Water and the latter primarily Equatorial-Subtropical Surface Water. Of 217 spotted and/or spinner dolphin schools encountered during the January-March cruises, and having associated temperature and salinity measurements, 80.6% were in this Tropical Surface Water, while only 19.4% were in the Equatorial-Subtropical Surface Water. In comparison 53.7% of 229 similarly observed schools of striped and/or common dolphins were in the Tropical Surface Water and 46.3% were in the Equatorial-Subtropical Water. The differential in percentages by species pair reflects the more uniform "Inner Tropical" Surface Water habitat of spotted and spinner dolphins and the importance to striped and common dolphins of both the variable Tropical Water off Central America and the variable waters along the Equator, west of Peru, and southwest of Baja California.

Because the school sighting data are represented by many combinations of temperature and salinity from various areas, it is useful to summarize these results in terms of an integrated measure of temperature and salinity, i.e., sigma-*t*, a measure of water density (see Sverdrup et al. 1942). Table 3 lists the numbers and percentages of spotted and spinner and of striped and common dolphins according to their occurrence at different intervals of sigma-*t*. The percentages of striped and common dolphin schools were higher than that of spotted and spinner dolphin schools for sigma-*t* ⩾22.5 (primarily Equatorial-Subtropical Water). The opposite was true for sigma-*t* <22.5 (primarily Tropical Water). The difference in percentage distribution by species pair is significant ($P < 0.01$, Kolmogorov-Smirnov test).

Seasonal Features of Habitats

It is not clear how dolphin populations are affected by seasonal changes in the environment, although the available data suggest what may happen. The far offshore habitat of spotted and spinner dolphins, between long. 120°W and 140°W at about lat. 10°N, is an important "porpoise-tuna" fishing area during

TABLE 3.—Percent distribution of dolphin schools[1] according to surface water density (sigma-*t*).

sigma-*t*	Spotted	Spinner[2]	Total	%	Striped	Common	Total	%
+18.5-19.0					2		2	0.9
+19.0-19.5	2	1	3	1.4	5		5	2.2
+19.5-20.0	6		6	2.8	8		8	3.5
+20.0-20.5				0.0	2	1	3	1.3
+20.5-21.0	5	2	7	3.2	6	2	8	3.5
+21.0-21.5	16	12	28	12.9	11	2	13	5.7
+21.5-22.0	43	28	71	32.7	27	6	33	14.4
+22.0-22.5	12	32	54	24.9	26	19	45	19.7
+22.5-23.0	15	6	21	9.7	22	8	30	13.1
+23.0-23.5	8	11	19	8.8	39	15	54	23.6
+23.5-24.0	2	4	6	2.8	10	3	13	5.7
+24.0-24.5	2		2	0.9	6	6	12	5.2
+24.5-25.0					1	2	3	1.3
+25.0-25.5								
Total	111	96	217	100	165	64	229	100

[1]January-March, research cruises, 1976, 1977, 1979, 1980.
[2]Includes mixed spinner + spotted dolphin schools.

the spring and summer months (Calkins 1975). However there is little information from that area during the winter months (when there is little fishing), except for results from the January-March research cruises, which indicated that population densities there were not high (Fig. 6). This suggests a summer buildup in the concentration of these dolphins. This is likely because the offshore habitat is centered close to or along the divergence zone at the northern boundary of the North Equatorial Countercurrent, where the thermocline ridges and biological production is increased (Cromwell 1958). During the northern summer, the trade winds over the offshore habitat abate, ridging intensifies (Wyrtki 1964a, 1974), and porpoise-tuna fishing expands west of Clipperton Island (at ca. lat. 10°N, long. 109°W). The increase in fishing may be due to better weather, but possibly also to an increased abundance of dolphins and tuna.

The seasonal change in environment of the eastern tropical Pacific most likely to affect the distribution of dolphins is that due to the movement of the southern border of the tropical waters. During the northern winter, tropical conditions usually extend to about 15° south of the Galapagos Islands, when a shallow surface layer of warm water develops over what is actually Subtropical Water. During the northern summer, the cool Peru and South Equatorial Current strengthen, and a conspicuous thermal front, marking the southern boundary of Tropical Surface Water, usually develops. This Equatorial Front (Wyrtki 1966) is located a few degrees north of the Equator except for a short section east of the Galapagos Islands.

We studied the relationship of the Equatorial Front to dolphin populations during an October-November 1977 cruise of the *David Starr Jordan*. The Equatorial Front was conspicuous, as were the effects of the cool Peru and South Equatorial Currents (Fig. 9). Only 4 of 27 sightings of spotted and spinner dolphins schools in the equatorial region occurred in the cool, Equatorial and Subtropical Waters south of the front. The majority of the remaining 23 sightings were along the Equatorial Front, at the southern border to the warm Tropical Surface Water. These same species had occurred throughout these southern waters during January to March (Figs. 3, 4), when sea surface temperatures of 25°C or more prevailed over this entire area. The apparent redistribution of dolphin schools along the warm edge of the Peru Current and Equatorial Front appeared to be restricted to the spotted and spinner species, suggesting their seasonal movements away from cool southern waters. By implication these same dolphin species may migrate into southern waters during the warm season. Seasonal movements of dolphins (unidentified) in the southern waters is also suggested by results from the 1967 and 1968 EASTROPAC cruises (Love 1971, 1972). On the other hand, we did see during the October-November cruise four schools of spotted and spinner dolphins in cool Subtropical Water, and observers aboard tuna seiners have also reported these same species there during the cool season.

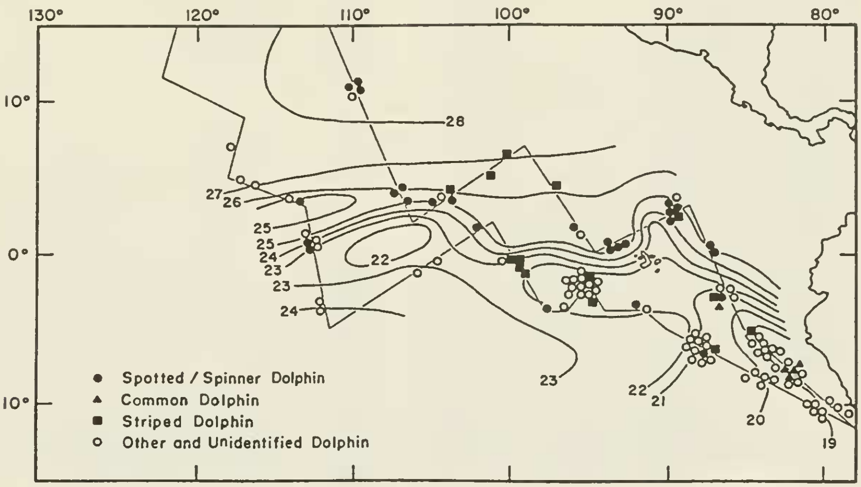

FIGURE 9.—Distribution of dolphin schools in the equatorial region during October-November 1977, relative to surface isotherms (°C). Notice the Equatorial Front or zone of rapid temperature change just north of the Equator. Clumping of sightings along the track is due to nighttime travel by ship. "Other" dolphins are primarily pilot whales.

Dolphin Communities

The habitat differences discussed also apply to other delphinid species, so that there seem to be different communities of dolphins in the eastern Pacific. To show how the cetacean communities differ between the habitats dominated by spotted and spinner and by striped and common dolphins, the eastern Pacific was divided into Areas I and II (Fig. 10, inset) that separate the main habitat areas of these two species pairs. Area I is primarily Tropical Surface Water and includes most areas where thermocline ridging is a dominant physical feature. Area II is primarily Equatorial-southern Subtropical Surface Water, but also includes the wedge-shaped area of variable Tropical Water in the Central American Bight. Area II comprises most of the waters we have called Upwelling-Modified.

In each of these two areas, only schools sighted at ≤1.0 nmi perpendicular to the ship's tracks were listed. This requirement was imposed so that percent species composition could be based on species schools, that to the largest practical degree, could all be sighted with equal probability, if present. The change in "sightability" with distance is different for each species because of differences in behavior, coloration, size, etc.

Our data indicate that the species composition of delphinids is different in these two areas. Percentage composition was determined for spotted; spinner; striped; common; bottlenose, *Tursiops truncatus*; rough-toothed, *Steno bredanensis*; and Risso's, *Grampus griseus*, dolphins, and for "blackfish", *Peponocephala electra/Feresa attenuata*; pilot whales, *Globicephala macrorhynchus*; and others (Table 4). Among 8 of 10 species-groups specifically identified in Table 4, there were significantly higher percentages of spotted, spinner, and rough-toothed dolphin schools in Area I than in Area II (Fig. 10). Risso's and bottlenose dolphins were important species in both areas, and their percentage values did not differ significantly between the areas. The percentages due to striped and common dolphins and pilot whales increased in Area II relative to Area I. Though reduced, the spotted dolphin remained important in the Area II dolphin community. The increase in percent composition of the common dolphin in Area II was not quite significant, reflecting the inclusion in Area I of that species' distributional lobe off Baja California. Overall, the species composition differed significantly between the two areas, as determined by chi-square contingency test of the frequency of species other than spotted, spinner, striped, and common, i.e., the species not initially considered when delimiting Areas I and II (χ^2 = 74.4, df = 5, $P <$ 0.005).

Additional evidence for the distinctiveness of the equatorial and subtropical portions of the Area II community is provided by observations along equatorial transects and transects south and south-

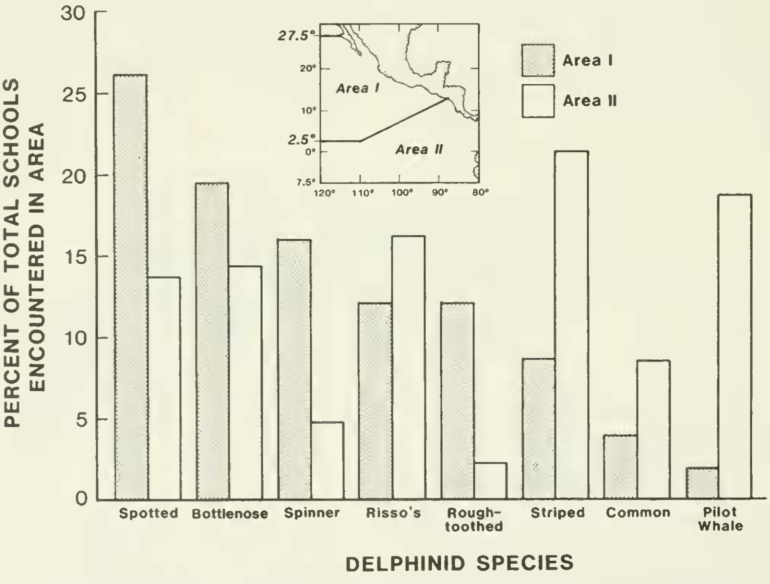

FIGURE 10.—Percent species composition of some important cetaceans, by Area I and II. See Table 4.

TABLE 4.—Percent composition of species as encountered in two areas[1] during the January-March research cruises.

Delphinid spp.[2]	Area I Schools	Area I %	Area I 95%[3] C.I.	Area II Schools	Area II %	Area II 95%[3] C.I.
Spotted, *Stenella attenuata*	67	24.7	19.6-29.8	55	13.2	10.0-16.4
Spinner, *Stenella longirostris*	41	15.1	10.8-19.4	19	4.6	2.6-6.6
Striped, *Stenella coeruleoalba*	22	8.1	4.9-11.3	86	20.6	16.7-24.5
Common, *Delphinus delphis*	10	3.7	1.5-5.9	34	8.2	5.6-10.8
Pilot whale, *Globicephala macrorhynchus*	5	1.8	0.2-3.4	75	18.0	14.3-21.7
Risso's, *Grampus griseus*	31	11.4	7.6-15.2	65	15.6	12.1-19.5
Bottlenose, *Tursiops truncatus*	50	18.5	13.9-23.1	58	13.9	10.6-17.2
Rough-toothed, *Steno bredanensis*	31	11.4	7.6-15.2	10	2.4	0.9-3.9
"Blackfish", *Peponocephala electra* or *Feresa attenuata*	8	3.0	1.0-5.0	1	0.2	0-0.6
Other	6	2.2	0.2-4.2	14	3.4	1.7-5.1
Total	271			417		

[1]Areas are shown in Figure 10.
[2]Species in mixed schools were tabulated separately.
[3]Normal approximation to binomial distribution.

east of the Galapagos Islands, i.e., off Peru. Unlike during the January-March cruises, physical oceanography was the primary task on most of these transects, hence the ships did not usually divert course toward the schools, and many schools could not be identified. Nevertheless some idea of the species compositions can be obtained. The observations (Table 5) showed that pilot whales and Risso's and bottlenose dolphins were frequently encountered species during October-December off Peru, and common dolphins were often seen near the coast. On the equatorial transects, between long. 85°W and 110°W, striped and common dolphins were the characteristic species. The common dolphin was seen most often near the Galapagos Islands. Pilot whales were relatively abundant during May-July 1981 in this equatorial section. West of long. 110°W along the Equator, pilot whales again were the most frequently encountered species. Interestingly, sightings of Fraser's dolphins, *Lagenodelphis hosei*, and "blackfish" (probably *Peponocephala electra*) were also relatively frequent, especially between long. 110°W and 145°W. These two species often school together and appear to prefer equatorial waters (Perryman et al.[4]). In the next section, another distinctive feature of equatorial waters will be brought out.

Dolphins, Birds, and Tuna

A conspicuous feature distinguishing the dolphin communities is the difference in the species-specific association with tunas. In the eastern tropical Pacific, spinner dolphins and especially spotted dolphins are found associated with "surface" yellowfin tuna. It is these two species, therefore, that are mainly affected by the porpoise-tuna fishery (Smith 1983). Surface tunas occur at the sea surface and can be caught by purse seine, trolling, and pole-and-line gear. "Deep tunas" of the same species are caught by longline gear, generally in and below the thermocline. Since these surface tunas drive food to the surface, making it available to certain seabirds (Ashmole and Ashmole 1957; Murphy and Shomura 1972), a reliable indication that tuna are accompanying a dolphin school is the presence of a bird flock. Birds are the most important cue used by fishermen to locate dolphin-tuna schools.

Birds do not occur equally among the different dolphin species. During the 1977, 1979, and 1980 January-March cruises (when the best bird observa-

[4]Perryman, W. F., D. W. K. Au, and S. Leatherwood. Manuscr. prep. Melon-headed whale, *Peponocephala electra* (Gray, 1946) (with notes on the pygmy killer whale *Feresa attenuata*). Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 5.—Number of schools for species seen along equatorial and southeastern Pacific transects.

Region:	Off Peru: 0-10°S, 83°-95°W		Equator: 2°N-2°S 85°-110°W			Equator: 2°N-2°S 110°-145°W		Equator: 2°N-2°S 145°-180°W
Ships:	*D. S. Jordan*	*Researcher*	*Ocean-ographer*	*Researcher*	*Reseacher*	*Ocean-ographer*	*Ocean-ographer*	*Ocean-ographer*
Dolphin spp. Dates:	Oct.-Nov. 1977	Oct.-Dec. 1981	May-July 1981	July-Sept. 1980	Oct.-Dec. 1981	Mar.-Apr. 1980	May-July 1981	Mar.-Apr. 1980
Unidentified	7	13	34	20	29	22	8	1
Spotted, *Stenella attenuata*	3	1	3	3		2	2	1
Spinner, *S. longirostris*	3		1	2		1	1	1
Striped, *S. coeruleoalba*	5	1	14	13	11	3	3	1
Common, *Delphinus delphis*	4	6	18	9	13			
Bottlenose, *Tursiops truncatus*	10	15	5	4	1		1	
Pilot, *Globicephala macrorhynchus*	14	9	14	4	3	16	5	7
Risso's, *Grampus griseus*	23	14	2		1	7		1
Rough-toothed, *Steno bredanensis*	1		1		1	4		1
Fraser's, *Lagenodelphis hosei*						7	1	1
"Blackfish", *Peponocephala electra* or *Feresa attenuata*	2		1			8		2
False killer whale, *Pseudorca crassidens*	1				1	1		2
Killer whale, *Orsinus orca*	1	1	1	2	3			

tions were taken), 70.7% of 167 spotted, spinner, or mixed spotted and spinner dolphin schools, sighted between lat. 5°N and 30°N (where most dolphin-tuna associations occur), had 10 or more associated birds (Table 6). We assume this minimum flock size indicates associated tuna, although we did not often actually see the tuna. For the same period and area, 30.6% of 49 common dolphin schools and only 1.6% of 64 striped dolphin schools were with 10 or more birds. The different percent occurrences indicate that tuna are most frequently associated with spotted and spinner dolphins and very seldom with the striped dolphin.

The bird species most numerous in offshore waters with dolphin schools are boobies (*Sula* spp.); wedge-tailed shearwaters, *Puffinus pacificus*; and sooty terns, *Sterna fuscata*. Frigate birds (*Fregata* spp.) are also closely associated with these dolphins, though their average flock size is only seven (Au and Pitman[5]). These bird species are all strongly dependent upon tunas in their feeding. Our observations are that the birds feed primarly in association with the fish, not the dolphins.

The dolphin-tuna-bird association appears to be area- as well as species-specific. Assuming flocks of ⩾10 birds indicate the presence of yellowfin tuna, this association seems to occur in all areas with higher relative abundance of spotted and spinner dolphins (Fig. 11). The association seldom occurs along the Equator, or in areas outside the traditional porpoise-tuna fishing grounds (roughly these are waters within the triangular-shaped area whose base is formed by the American coasts between lat. 25°N and 15°S, and whose apex is at lat. 10°N, long. 150°W; see Calkins 1975 and IATTC 1979-81), even though the required species of dolphins, tuna, and birds may be present there. Relatively few of the spotted or spinner dolphin schools sighted near the Equator were with bird flocks. South of the Equator and in the Central Pacific, there are abundant flocks of sooty terns with fish schools, but dolphins do not usually co-occur (Au and Pitman fn. 5). The most important area of the dolphin-tuna-bird association is centered about the divergence zone near lat. 10°N, an important porpoise-tuna fishing ground for yellowfin tuna (primarily Area I of Figure 10).

These areal changes in the interactions among species are usually clearly apparent during north-south transects across the eastern Pacific during any season. An example is the July-September 1980, NOAA ship *Researcher* transits between Manzanillo, Mexico, and lat. 3°S, long. 100°W, via Clipperton Island. At that time Tropical Surface Water ($T > 25°C$) extended to the Equator with transition toward Equatorial Water marked by temperature and salinity fronts at lat. 5°N-6°N and at the Equator (Fig. 12). In the tropical waters north of the front at lat. 5°N there was a conspicuous increase in abundance of flocks of sooty terns, boobies, and shearwaters (*Puffinus* spp.), all broadly centered about the thermocline ridge at lat. 10°N. The larger gadfly petrels (*Pterodroma* spp.) were also abundant. All of these birds frequently flock over fish and dolphins. South of this boundary was another avian group, with *Pterodroma leucoptera*, a small petrel from the Southern Hemisphere, and planktivorous storm petrels (*Oceanodroma* spp.) predominating, and peak abundances at the Equator. These latter birds usually feed independently of fish and seldom flock over fish and dolphins.

Correlations among water masses, seabirds, and the different cetaceans along the transect were difficult to quantify because of the small sample size of the latter. However, the observations are supportive of such relationships. There were 39 dolphin schools, of which 15 were unidentified, and 21 whale schools along this transect. Spotted and spinner

[5]Au, D. W. K., and R. L. Pitman. Manuscr. prep. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 6.—Dolphin schools associated with seabirds.

	5°N-30°N			<5°N		
Dolphin spp.	Schools	with ⩾10 birds	%	Schools	with ⩾10 birds	%
Spotted	95	56	58.9	40	8	20.0
Spotted and spinner	55	53	96.4	21	8	38.1
Spinner	17	9	52.9	19	6	31.6
Common	49	15	30.6	10	1	10.0
Striped	64	1	1.6	76	1	1.3
Rough-toothed	40	5	12.5	13	1	7.7
Other/unidentified	388	17	4.4	189	6	3.2

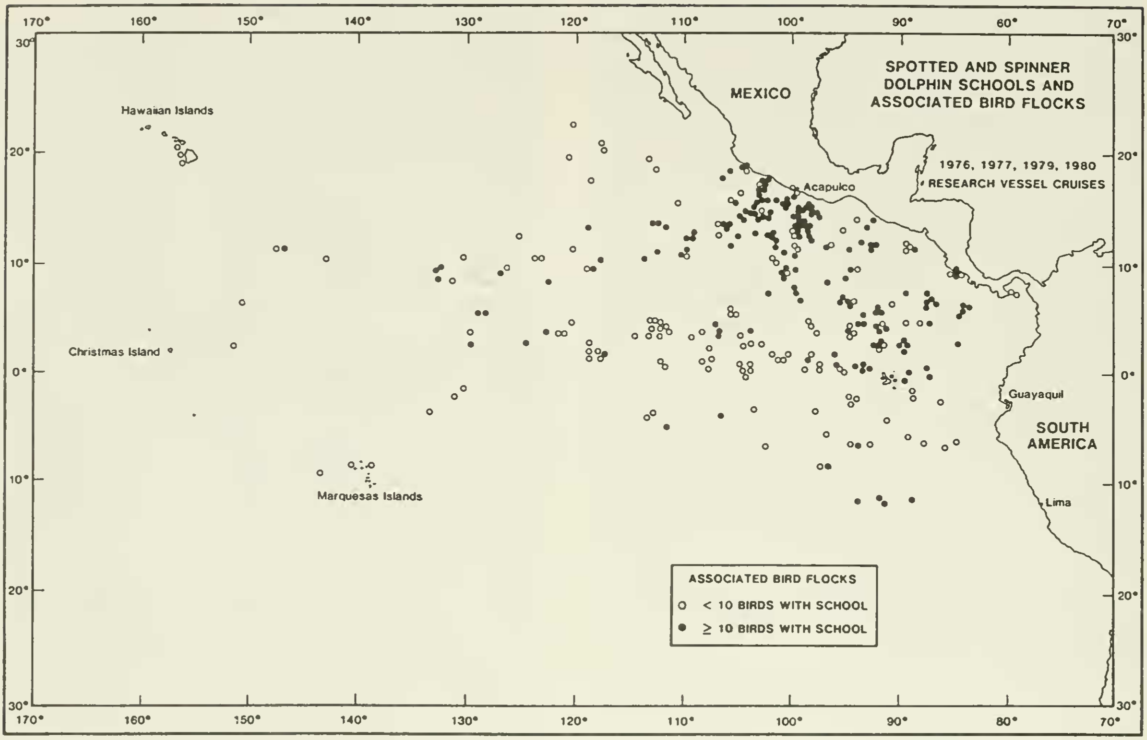

FIGURE 11.—Distribution of bird-associated spotted and spinner dolphin schools during the January-March research cruises. Schools with 10 or more birds are assumed to be with tuna.

dolphns did occur coincidentally with bird flocks (and probably with tuna) in the warmer tropical waters centered about lat. 10°N, but also were seen at the Equator, though without associated bird flocks. Striped and common dolphins occurred in coastal and equatorial waters, without bird flocks. These latter dolphins were the characteristic species on the equatorial transect of this same cruise (see Table 5, col. 4), where only one of the schools seen, a mixed spotted and spinner dolphin school, had an associated bird flock. The distinct change in the bird fauna south of lat. 5°N to species that do not forage commensally with fish suggests there are changes with water masses in the nature of epipelagic prey and how the top predators forage.

DISCUSSION

It should not be surprising that the two major divergence zones of the eastern Pacific, near lat. 10°N and along the Equator, are important features of the oceanic habitats of eastern Pacific cetaceans. Enriched by the effects of wind and the major zonal currents (Brandhorst 1958; Cromwell 1958; Reid 1962; Wyrtki 1966), the zones are evident areas of enhanced biological production (Blackburn 1966, 1976; Blackburn et al. 1970; King 1974; Parsons et al. 1977; Brinton 1979). that are important to tunas (Calkins 1975; Blackburn 1965; Blackburn and Laurs 1972; Blackburn and Williams 1975; Sund 1981) and cetaceans as discussed above. These two zones are not qualitatively the same, however; the strong, shallow thermoclines that have been related to successful porpoise-tuna fishing (Green 1967; Miller et al.[6]) and to aggregations of dolphins and baleen whales (Rovnin 1969; Volkov and Moroz 1976) are characteristic of the lat. 10°N zone, but not of the Equator. Similarly the oxygen minimum layer, noted by Perrin et al. (1976) to be correlated with the distribution of the spotted dolphin, occurs only north and south of the Equator in the eastern Pacific. Equatorial waters are characterized by shallow, weak (<2°C/10 m) thermoclines, due to upwelling and the Equatorial Undercurrent, and cool surface temper-

[6]Miller, F. R., C. J. Orange, R. H. Evans, and K. A. Bliss. Manuscr. prep. Analysis of environment related to tuna fishing in ETP. Inter-American Tropical Tuna Commission, La Jolla, CA 92038.

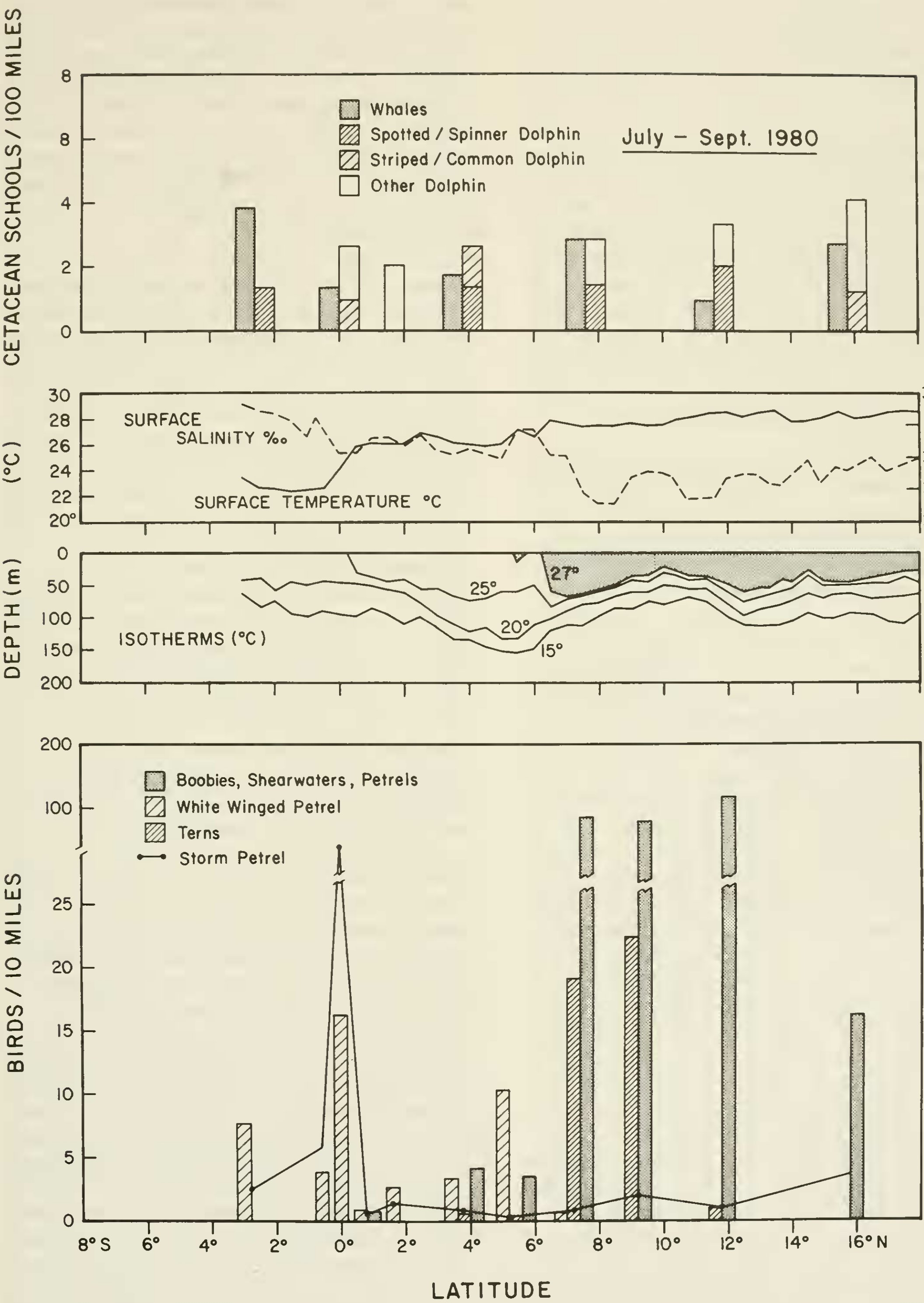

FIGURE 12.—Transect along long. 110°W, July-September 1980, showing changes in cetaceans, birds, and temperature and salinity. The relative abundance of dolphin schools include unidentified schools which were prorated according to species ratios of identified schools.

ature from June through December. These waters support a different cetacean community (Table 5), though school densities there can be as high as in areas off Mexico and Central America (Au et al. 1980).

Other relationships between distribution and movements of dolphins and water masses, convergences, and thermal conditions have been described by Fraser (1934), Gaskin (1968), Kasuya (1971), Nishiwaki (1975), Evans (1975), and Miyazaki and Nishiwaki (1978). Hui (1979) found that common dolphins off California tended to occur over prominent features of bottom topography. The deep depths of such areas suggest that surface eddies and convergences caused by topography-induced accelerations to deep reaching currents (Sverdrup et al. 1942; Neumann 1960) may have concentrated food and attracted the dolphins.

The distributions of dolphin species as seen from the January-March cruises (Figs. 3-7) are similar to the all-season school distributions derived from data of scientific observers aboard tuna seiners. These data, consisting of thousands of sightings per species, were recently summarized by Scott (1981) and Perrin et al. (1983). The same major distributional patterns as presented here for the January-March cruises were apparent, including, for spotted and spinner dolphins, the relative unimportance of equatorial latitudes and the secondary band of increased concentration of schools 2°-5° north of the Equator. The latter may be related to the Equatorial Front and increased food concentration and possibly production in the convergence zone there (Sette 1955; King and Iverson 1962; Blackburn and Laurs 1972; Murphy and Shomura 1972; Pak and Zaneveld 1974; Blackburn and Williams 1975; Greenblatt 1979). Increased abundance of micronekton occurs at least sometime in this zone (Love 1971, 1972; Blackburn and Laurs 1972). The purse seiner data, like those of this paper also showed spotted and spinner dolphins more concentrated in the tropical waters off Mexico and along lat. 10°N, while striped and common dolphins tended to be found in the Central American Bight and along the Equator. This complementary type of distribution was less apparent with the more broadly distributed striped dolphin. It should be noted that our southern distributional lobe for spotted and spinner dolphins, at ca. lat. 5°S, may in part be due to the sampling pattern. However, the density of these dolphins along the Equator is definitely reduced, and we know of no information that does not suggest a rapid decline in density south of our lobe.

Our January-March data differs from the all-season data in indicating fewer schools in the area around the Revilla Gigedo Islands (at ca. lat. 19°N, long. 111°W) and between long. 90°W and 100°W along lat. 10°N for spotted and spinner dolphins. Also our data suggested that striped and common dolphins had a more localized distribution near the region of the Costa Rica Dome, and were relatively infrequent between long. 105°W and 120°W, along lat. 10°N. These differences may be due to seasonal changes in distribution.

The relative densities of these dolphins, as school encounter rates in the tuna purse seine fishery, were recently calculated by Polacheck (1983). The patterns he derived were fragmentary, but not inconsistent with those of this paper. He showed, for example, higher densities of spotted and spinner dolphins extending to the southwest from off southern Mexico and reduced densities in the Central American Bight. For striped and common dolphins, he also described a three-lobed distribution pattern as in this paper. However his equatorial lobe was centered just south of the Equator.

It seems likely that the dolphin community of the Upwelling-Modified Water differs from the Tropical Water community because of water-mass specific differences in the distribution and availability of food. This is supported by the different biotic features of Equatorial and Subtropical Waters relative to Tropical Waters. The distinction is clearly shown by the surface distribution of nutrients and primary production in these waters as measured during the EASTROPAC cruises (Love 1971, 1972). The equatorial waters of the eastern Pacific in particular are different. They support abundant plankton-feeding storm petrels rather than fish and cephalopod-feeding flocking birds that are usually abundant both north and south of the Equator (see also Love 1971, 1972 and King 1974). Dolphin species along the Equator tend not to be with fish or birds (Figs. 11, 12), and the species composition of the cetacean community appears to be distinct (Table 5; Au and Pitman 1981). Of course it has previously been known that equatorial waters are notable in being important sperm whale grounds (Townsend 1935) and have a zooplankton community distinct from other parts of the eastern tropical Pacific (McGowan 1972). Finally the fact that the common dolphin, a species characteristic of coastal upwelling waters from California to Peru, occurs with greater frequency in the equatorial waters and near upwelling areas in the Central American Bight, suggests that the shorter and different food chains of the upwelling environments (Parsons et al. 1977) may be the basis of the community difference.

The dolphin-tuna-bird association is one manifestation of community difference that is both striking and of ecological interest. The distribution of this association is notable in that it seems coincident with both the main habitats of spotted and spinner dolphins and the distribution of "surface" yellowfin tuna in the eastern Pacific (see Figure 11, Shingu et al. 1974, and Suzuki et al. 1978). Since it is primarily these dolphins that are associated with birds and with yellowfin tuna, the geography of the dolphin-bird association also defines that of the dolphin-yellowfin tuna association. This association of birds and fish with dolphins occurs in all tropical waters, including the southern Subtropical Water during the southern summer. It is apparently rare in equatorial waters of the eastern Pacific, in the central and western Pacific (Myazaki and Wada 1978; Au et al. fn. 2), and in the eastern tropical Atlantic (Levenez et al. 1980). In the central Pacific the same bird species found with spotted and spinner dolphins in the eastern tropical Pacific can be abundant (Gould 1974), and sooty terns especially, are frequently associated with small tunas, but these are most likely skipjack tuna (Murphy and Ikehara 1955; Waldrom 1964; Hida 1970; Blackburn and William 1975). Apparently those flocks seldom accompany dolphins or schools of larger yellowfin tuna. Yellowfin tuna and dolphins seldom seem to associate outside the eastern tropical Pacific.

The obvious feeding activity often seen in these joint aggregations of birds, spotted and spinner dolphins, and tuna suggests that these species have similar food and foraging requirements. Our observations indicate that the mammals and fish are not tightly associated in the aggregations (see Au and Perryman 1982) and probably feed independently (see also Norris and Dohl 1980a). However the tuna, birds, and spotted dolphin (at least) do appear to be feeding at the same time. Both the tuna and spotted dolphins feed on epipelagic fish and on squids (Perrin et al. 1973; Olson 1982), but the spinner dolphins feed differently and may forage more at night (Perrin et al. 1973; Norris and Dohl 1980b); though they are active in these feeding aggregations, they may not be directly associated with the tuna. Judging from the associations of bird and dolphin species, only spotted and spinner dolphins frequently find it advantageous to feed with yellowfin tuna. Furthermore the distribution of this association suggests that the necessary kind and behavior of prey that is likely the basis of the association appears characteristic of tropical, but not equatorial, waters. It occurs especially where a shallow thermocline may constrain the yellowfin tuna to the surface layer with the dolphins, a complex interaction between environment and physiology (Sharp 1978) that may cause the phenomenon known as "surface tuna". Finally the distribution of the bird-dolphin association indicates that the dolphin-tuna association is characteristic of areas of higher school density of spotted and spinner dolphins. High population densities of both dolphins and yellowfin tuna, and suitable prey are therefore likely requisites for joint dolphin-tuna schools. The dolphin-tuna association is a feature of the most productive tuna fishing zones of these tropical seas. In such rich areas, feeding tactics to exploit clumped prey could lead to multispecies aggregations of predators, as explained by Schoener (1982).

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